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CONTENTS

Pollen grains in the identification and classification of plants—III. The Nassauvinae (plate 3) ..... ROGER P. WODEHOUSE 123
A double-walled pot for the auto-irrigation of plants ..... J. DEAN WILSON 139
Development of the integument and germination of the seed of Eleusine indica ..... MARGARET P. CUMMINS 155
New plants from Nevada ..... PHILIP A. MUNZ 163
INDEX TO AMERICAN BOTANICAL LITERATURE 169

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Pollen grains in the identification and classification of plants
III. The Nassauvinae

ROGER P. WODEHOUSE

(WITH PLATE 3)

A study of the pollen grains of the Compositae has shown that, though the family as a whole is characterized by much uniformity and closeness of relationship there exists within it a wide range of pollen-grain forms. The differences in the size, shape, texture and adornments of the grains of the different species are sometimes truly enormous; still the grains are all stamped with a 'family resemblance' which is in keeping with the various degrees of interrelationship.

Though the Compositae are the largest and most clearly defined of all the families of the flowering plants, there is much uncertainty as to the relationship of the various tribes and subtribes to each other, and of the relations of the family as a whole to other families. Nevertheless the pollen grains of the various tribes and subtribes generally possess certain characters which distinguish them readily enough from those of others; and since these characters, when compared throughout groups of the Compositae of known relationships, show more or less definite trends of genetic development, it is to be expected that their further study will throw some light upon the more obscure or doubtful relationships, and possibly by projecting backwards these known lines of development, suggest the origin of the family as a whole.

The characters of pollen grains belong in a category quite apart from that of the grosser anatomical structures, though of similar phyletic distribution. Harper (1913) has shown in his studies of *Pediastrum* that 'specifically inherited cell form and cellular interactions during growth are the principal morphogenetic factors in the development of the differentiated cell colonies,' and he has shown that the number of cells and consequently their arrangement in the colonies is, to a certain extent, a matter of individual variation and of little use in the identification or classification of the different species, but that the degree to which the spines of the individual cells develop

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affords a basis for the delimitation of species, and further (1918) the number of the spines on each of the peripheral cells of the colony affords the means of making the major divisions of the genus. The laws which Harper has established for *Pediastrum* are universal, but in the highly organized plant body of the phanerogams the specifically inherited cell forms of tissue cells are largely prevented, by their interactions with their neighbors and their subservience to their functional requirements, from coming individually to expression; so that in studying the completely organized plant body we are dealing mainly with the results of the inherited 'cellular interactions' further modified by outside environmental conditions, which is but half the story. The other half, the specifically inherited cell form is to be found in the pollen grains which are comparatively much less modified by cellular interactions and certainly bring to expression their specific capacities in a freer environment than that of the somatic cells. Consequently most of the characters of pollen grains are those of the specifically inherited cell form.

Making use of the characters of the pollen grains, which have hitherto been neglected in all phylogenetic studies of the Compositae, it is the purpose of the present series of studies to see to what extent the pollen-grain characters will substantiate or refute the current ideas of the classification of the family. The results obtained from my previous investigations of the Ambrosiaceae and of *Barnadesia* encourage me to hope that a similar study of the pollen-grain forms of all the groups of the Compositae will help to establish the interrelationships of the various tribes and the origin of the group as a whole. With this in view the present paper presents an analysis of the pollen-grain forms of one of the subtribes of the Mutisieae, the Nassauvinae.

HABIT AND DISTRIBUTION OF THE NASSAUVINAE

The Nassauvinae constitute rather an isolated group of Compositae, comprising some hundred and seventy-five species in fifteen genera. Their relationships with the rest of the family are somewhat uncertain; their corollas, always distinctly bilabiate, are those of the Mutisieae, but their style branches, except in *Proustia*, 'tronquées et penicellées à l'extrémité,' are those of the Senecioneae, to which group in some genera, the

involucre and general habit bear a close resemblance. Nevertheless there is no doubt in the minds of most botanists that the Nassauvinae belong properly in or near to the Mutisieae.

In distribution the Nassauvinae are almost entirely confined to the western part of South America or, more especially, to the extratropical or Chilean region, which is the one region in the world where the Mutisieae are the dominant Compositae, comprising nearly one third of all the family. A few genera of the Nassauvinae, however, are represented fairly abundantly in the Andean region to the north; a few reach through the mountainous regions of Central America and Mexico, and two genera are represented even in the southwestern part of the United States. Some species of *Jungia* are native of Brazil and Colombia, and one species of *Perezia* is found on the shores of Tierra del Fuego. Roughly speaking they reach from California to Cape Horn, with their greatest concentration of species and individuals in the Andean region.

Of the fifteen genera included in the Nassauvinae the pollen from species of eleven genera has been examined. These eleven genera are described below.

Jungia Linn. f. comprises about twelve species in Chile and Brazil, a few extending as far north as Colombia. The plants of this genus have much of the habit and occasionally the involucre of the Senecioneae, but they are mutisiaceous in their essential characters, and are regarded by Bentham and Hooker (1873) as most closely related to the next genus.

Trixis P. Browne comprises about eleven species, mostly shrubs of diverse habit but frequently resembling the Senecioneae. A genus of wider distribution than *Jungia*, *Trixis* reaches from Chile through Central America to Mexico and the West Indies, and two species are found in the southwestern part of the United States.

Nassauvia Jus. comprises about twenty-five species of low sprawling shrubs. In some the leaves are closely appressed, giving the branches a scaly serpent-like appearance; in others they are spreading and spine-tipped. The species of this genus are confined to the Chilean Andes, Patagonia, and the Falkland Islands, with one species reported from Cape Horn (Macloskie, 1906).

Triptilion Ruiz et Pav. comprises about six species confined

to the Chilean region and Patagonia, annual and perennial herbs of various habit, but in essential characters scarcely different from *Nassauvia*.

Proustia Lag. comprises about six or seven species in the

TABLE 1

Pollen-grain characters of the Naussavinae

NO TRACE OF SPINES IN ANY SPECIES, TEXTURE ALWAYS FINELY BUT DISTINCTLY GRANULAR	SHAPE			FURROW						SIZE IN MICRONS
	Spheroidal	ellipsoidal	flattened	tapering	rounded	flecked	marginate	transverse furrow	polar elev.	
Jungia pauciflora Rusby	+			0	+	+	+	0	0	27.5
J. floribunda Less.	+			0	+	+	+	0	0	25.8
Trixis involucrata D. Don		+		0	+	+	0	0	+	30.0×42.5
T. frutescens Spreng.[a]		+		0	+	+	0	0	+	24.0×33.0
T. corymbosa D. Don		+		0	+	+	0	+	+	30.8×43.3
T. angustifolia DC.		+		0	+	+	0	0	+	30.0×40.0
T. radialis (L.) O. K.[a]		+		0	+	+	0	+	+	25.3×37.5
Proustia pungens Poepp.	+			0	+	+	0	0	0	40.0
P. Krugiana Urban	+			0	+	+	0	+	+	26.6
P. pyrifolia Lag.	+			0	+	0	0	+	sl	28.6
P. Vanillosma Wright	+			0	+	+	0	+	+	30.0
Perezia Wrightii A. Gray	+			0	+	+	0	+	0	32.5
Nassauvia pyramidalis Meyen var. arachnoidea O. K.			sl	0	+	+	0	0	0	25.0
N. pungens Phil.			sl	0	+	+	0	0	0	27.0
N. serpens Urv.			sl	0	+	+	0	0	0	22.5
Triptilion euphrasioides DC.			sl	0	+	+	0	sl	0	18.5
T. Benaventii Remy			sl	0	+	+	0	sl	0	24.2×18.7
T. cordifolium Lag.			sl	0	+	+	0	sl	0	18.1×16.5
T. spinosum Ruiz & Pav.			sl	0	+	+	0	0	0	23.0
Pamphalea bupleurifolia Less.	+			+	+	0	0	sl	0	19.8
P. heterophylla Less.	+			+	+	0	0	sl	0	19.8
Cleanthes brasiliensis D. Don	+			+	0	+	0	sl	sl	27.3
C. hieracoides Griseb.	+			+	0	sl	0	0	0	21.9
C. hieracoides D. Don	+			+	0	sl	0	sl	0	20.9
Polyachyrus sphaerocephalus D. Don	+			+	+	0	0	0	sl	27.5
Leuceria tenuis Less.	+			+	+	0	0	0	0	19.4
L. paniculata Poepp.	+			+	+	0	0	0	0	27.5
L. anthemidifolia O. K.	+			+	+	0	0	0	0	23.0
L. purpurea Hook. & Arn.	+			+	+	0	0	0	0	25.8
Moscharia pinnatifida Ruiz & Pav.	+			+	+	0	0	0	0	30.0

[a] *Trixis frutescens* Spreng. has often been regarded as a synonym of *T. radialis* (L.) O. Kuntze, but recent study indicates that both species may be maintained, which is also indicated by the pollen-grain size.

Chilean region with a few in Mexico and one in Cuba. They are mostly erect shrubs or climbers, superficially resembling some Gochnatinae but are easily distinguished from that subtribe by their decidedly bilabiate corollas, a character nearly or

quite lacking in the Gochnatinae. Their style branches differ from those of all other Nassauvinae in their rounded tips, but conform to the subtribe in their long spreading form. The genus has a similar distribution to, and is regarded by Bentham and Hooker as most nearly related to *Perezia*.

Perezia Lag., the largest and possibly the most wide-spread genus, comprises forty-six species, mostly low coarse herbs, frequently with spine-tipped leaves resembling holly. Most of them are confined to the high cordilleras of South America, but a few are found in Mexico and even in the southwestern part of the United States, a few in Brazil, and in Patagonia as far south as Cape Horn.

Pamphalea Lag. comprises four or five species of annual herbs erect and branching, confined to the Chilean region. The flowers are white, borne in small heads on long peduncles. The corollas are distinctly bilabiate, but the lips are generally nearly entire, lacking the two teeth of the upper and the three of the lower lip, which are well developed in most other Nassauvinae.

Cleanthes D. Don comprises four or five species confined to Brazil. In some respects they are similar to *Trixis*, and are included in that genus by Bentham and Hooker, but in other respects they are quite different and are regarded as a separate genus by Don (1829), who says 'This genus, which appears to be a very natural one, is essentially distinguished from *Trixis* by the naked receptacle,' and by Grisebach (1879, p. 216) who says that the genus is distinct, unnaturally ('invita natura') joined with *Trixis*. The plants are perennial herbs with the flowers borne in many headed corymbs on slender stems bearing few scattered sessile leaves and with larger petioled leaves at the base, after the fashion of many hawkweeds. Thus in habit they stand in marked contrast to the species of *Trixis*, which are all shrubs. The flowers of *Cleanthes* also differ from those of *Trixis* in the shorter elliptical and more minutely toothed lower lip of the corolla, and in their pappus, which is persistent, while in *Trixis* it is caducous. It will be shown that the difference between these two genera is strongly expressed in the characters of their pollen grains.

Polyachyrus Lag. comprises about seven species, annual or perennial herbs, generally very woolly or glandular-hairy. The species are about equally divided in distribution between

southern Peru and the northern provinces of Chile. The genus is very distinct, but approaches, at least in outward appearance, certain species of *Leuceria*, and is regarded by Bentham and Hooker as most closely related to that genus, though Weddell (1835) following Cassini, insists that the relationship is most closely with *Nassauvia*. As we shall see, the evidence of their pollen grains is decidedly in favor of the former view.

Leuceria Lag. comprises about twenty-five species confined almost entirely to the Chilean region, annual or perennial herbs with leaves more or less downy white; of various habit, but sometimes resembling the Cichoriaceae.

Moscharia Ruiz et Pav. consists of but a single species in Chile, an annual herb, in outward appearance bearing some resemblance to *Leuceria*. The name *Moscharia* is well chosen from the odor of musk which the whole plant gives off. This same character also suggests the common name, Almizqcillo (Ruiz et Pavon, 1797, p. 91).

The characters of the pollen grains of thirty-two species of these eleven genera are displayed in table 1. It is seen that the grains of all species within each of the different genera, except for some variation in size, are essentially alike.

The distribution of the characters among the different genera is summarized in the following key. The grouping of the genera on the basis of these characters, brought out by the arrangement of the key, concurs with the classification of Bentham and Hooker; therefore it may be regarded as natural, and shows that the pollen-grain characters of these plants are correlated with the other anatomical characters.

KEY TO THE DISTRIBUTION OF THE POLLEN-GRAIN CHARACTERS

Grains entirely psilate, no trace of spines found in any species; furrows always sharply defined and extremely long, almost meeting at the poles, more or less rounded at the ends or sharply pointed (in *Cleanthes*); texture finely but conspicuously granular. Grains sphaeroidal, slightly flattened, or ellipsoidal, not conspicuously lobed, and always lacking intercolpar thickenings and concavities; various in size from 18.5μ to 40.0μ transverse measurement.

A. Furrows scarcely tapering, broadly rounded at the ends and flecked with more or less conspicuous granules.

Furrows marginate, grains approximately spheroidal.... *Jungia* (fig. 1)

Furrows emarginate

Grains ellipsoidal with prominent polar elevations.. *Trixis* (figs. 2, 3)

Grains spheroidal with or without slight polar elevations... *Proustia*
Perezia

Grains slightly flattened, without prominent polar elevations ..... *Nassauvia*
Triptilion (fig. 4)

B. Furrows tapering to a more or less rounded end, sharply pointed in *Cleanthes*, approximately spheroidal.

Furrows more or less flecked ..... *Pamphalea*
Cleanthes

Furrows not flecked ..... *Polyachyrus* (fig. 5)
Leuceria
Moscharia

POLLEN GRAINS OF THE NASSAUVINAE

The pollen grains of the Nassauvinae (figs. 1–5) are notable among the Compositae for two well marked characters, the absence of spines and the extreme development of the furrows. Not even the smallest vestige of spines has been found in any of the species examined; and the furrows are always sharply defined and extremely long. The lengthening has been carried to such an extent that they almost meet at the poles, the approaching ends of neighboring furrows being separated by only a narrow isthmus of unmodified exine, often less in width than the furrows themselves. There is considerable variation among the grains of the different species in the amount of tapering of the furrows towards their ends, but in those of all except one genus, the furrows are more or less rounded at the ends, and in many they are as broad at the ends as in the middle. These two characters, the entire absence of spines and the extremely long sharply defined and usually rounded furrows, are together quite distinctive for the pollen grains of the Nassauvinae, and serve to distinguish them from all the rest of the Mutisieae or the Compositae so far examined.

In other characters the pollen grains of the Nassauvinae are also rather sharply set off from the rest of the Mutisieae. In texture all are distinctly but finely granular, showing little variation in this respect, and lack entirely the coarse pebbled appearance characteristic of the grains of most of the other Mutisieae. In size they are small, ranging from 18 to 40 microns in diameter, and nearly all are less than 30 microns, while in the other tribes of the Mutisieae the size ranges as high as 57 microns in diameter, with the majority well above 30 microns. Thus the pollen-grain characters indicate that the group is rather compact and distinct from the rest of the tribe.

The pollen-grain forms of the Nassauvinae fall into two rather well marked groups as indicated in the key: those in which the furrows taper scarcely or not at all to their broad rounded ends and have the furrow surface always conspicuously flecked (group A); and those in which the furrows taper quite distinctly to their ends, which are nevertheless generally somewhat rounded, except in some species of *Cleanthes*, and have the furrow surface smooth or only occasionally slightly flecked (group B).

The tapering of the furrows is not alone always distinctive, for in both groups are encountered borderline cases, but the presence of flecks on broad nontapering furrows is quite distinctive and serves to separate the grains of *Jungia*, *Trixis*, *Nassauvia*, *Triptilion*, *Proustia*, and *Perezia* (group A) from those of the other genera of the subtribe.

The furrow flecks present the same staining properties as the cutinized material of the outer layer of the exine, as though, at the time of formation of the furrow, small fragments of the outer layer of the exine had become detached and left distributed over the surface of the furrow.

The presence of these flecks undoubtedly bears some relation to the closing of the furrow, and is probably the outcome of the lack of efficiency in closing, arising out of the broad and rounded ends of the furrows with which they are generally associated in this group. It will readily be seen that furrows of this character in the semirigid material of the exine, cannot close tightly and must remain gaping at least at the ends. Such was actually observed to be the case in some abortive and unexpanded grains. It has been shown by Tischler (1908) and others that in sterile hybrids when pollen cells abort during sporogenesis, if the abortion takes place after the rudiments of the exine have been laid down, its development is carried to completion in every detail, even though the pollen cells remain empty. It so happens that in the pollen of many normal species a few grains are to be found that are abortive and empty, yet displaying all the external details with even greater brilliancy than do the normal grains, and these remain unexpanded during staining and embedding. A striking example of this was found in the pollen of *Trixis angustifolia*, in which many grains are abortive. In the normal expanded

grains towards the ends of the furrows the flecks are numerous and close together, but in the mid-region of the furrow they are few and scattered. The explanation of this is apparent in the unexpanded grains, for in these the edges of the furrows are seen to nearly touch in the middle, but gape considerably towards the rounded ends. Nevertheless the furrow, so contracted, is tightly and evenly packed with flecks throughout its entire length. When such a furrow expands and its sides become parallel or slightly convexed, the elastic membrane bearing the flecks is stretched and in the mid-region of the furrow where the stretching is greatest, the flecks are most widely separated, while towards the ends where the stretching is less they are but little separated.

The way in which the flecks are distributed is various in the different species, sometimes offering a good specific character. For example, in the grains of *Triptilion cordifolium* and *T. spinosum*, they cover a narrow strip extending the full length and exactly in the center of the furrow, while in *T. euphrasioides* and *T. Benaventii* they are simply scattered.

The presence or absence of the rounded flecked furrow appears to indicate quite a natural division of the subtribe, for, according to the classification of Bentham and Hooker, *Jungia*, *Trixis*, *Nassauvia*, *Triptilion*, *Proustia*, and *Perezia*, the plants possessing this character (group A), are each more closely related to the other than they are to the remaining genera of the subtribe.

The grains of *Jungia* (fig. 1) are distinctly set off from those of the other five genera of group A by the possession of a slightly overhanging fold along the margins of the furrows; they are distinctly though finely granular, with the granules appearing to coalesce at the base of the overhanging part of the margins. Marginate furrows of this character are not found elsewhere in the tribe, and together with the small size, nearly spherical form, and absence of spines they serve to distinguish the grains of *Jungia* from those of all other genera.

The grains of the six species of *Trixis* (figs. 2, 3) that were examined are all essentially alike and easily distinguished from those of the other genera by their elongate form and their possession of very pronounced polar elevations, a character which reaches its maximum development in this genus. These

grains are remarkable for their large size and elongate form (table 1); in most species they are fifty per cent or more longer than broad. The long furrows are carried without appreciable tapering well up into the polar elevations. The transverse furrow is usually well defined and conspicuous. These grains present rather a striking appearance not easily confused with those of any other genera.

The grains of all species of *Proustia* and *Perezia* that have been examined are essentially alike, distinguished from those of *Trixis* and of the two following genera by their spheroidal form, and from those of *Trixis* also by their weaker development or entire absence of polar elevations. It is interesting here to note that *Proustia* is stated by Bentham (1873) to be 'very nearly allied to *Perezia*' in the Nassauvinae, but is placed by Hoffmann (1893, p. 341) next to the Chinese *Nouelia* Franchet in the subtribe Mutisinae. A comparison of the pollen grains of *Proustia* with those of the various members of the two subtribes shows that they differ distinctly from those of the Mutisinae in the absence of spine vestiges, their surface texture and their long rounded flecked furrows. In these characters, however, they harmonize perfectly with the Nassauvinae, and are almost indistinguishable from the grains of *Perezia*. So there can be little doubt of the incorrectness of Hoffmann's view in placing *Proustia* in the Mutisinae, and the correctness of Bentham's in associating it with *Perezia* in the Nassauvinae.

The grains of all species of *Nassauvia* and *Triptilion* (fig. 4), genera which are always regarded as closely allied, are indistinguishable from each other, but are easily distinguished from those of *Trixis*, *Proustia*, and *Perezia* by their flattened form and entire absence of polar elevations.

Looking back over these six genera of our group A in the key, it is seen that according to the evidence of the pollen grains, the last four genera of the group are all rather closely related, *Proustia* and *Perezia* being distinguished from *Nassauvia* and *Triptilion* only by the slightly flattened form of the grains of the two latter. The grains of *Trixis* (figs. 2, 3), however, differ from them rather widely in general appearance. They are larger, much longer and possess more prominent polar elevations, altogether presenting an appearance strikingly different from the grains of the other four genera. These

differences, however, are only of degree, involving characters which are also present to a certain extent in the grains of the other four genera. On the other hand the grains of *Jungia*, though in general appearance more like the grains of *Proustia*, are distinguished from them by the possession of marginate furrows, a character which is not even suggested in the grains of *Proustia*, *Perezia*, *Nassauvia*, and *Triptilion*. For this reason *Jungia* is more widely separated from them in the key than is *Trixis*. Whether this view is correct or not can best be decided by seeking intermediate forms; it is quite possible that among the many species of *Trixis* that have not been examined, grains will be found that are smaller, less elongate, and with less prominent polar elevations, or that among those of *Jungia* grains will be found with emarginate furrows. However this may be, the evidence of the pollen grains so far presented indicates that the six genera of group A are more closely related to each other than they are to the following group.

The remaining genera, *Pamphalea*, *Cleanthes*, *Polyachyrus*, *Leuceria*, and *Moscharia*, group B in the key, reveal much less of their interrelationships through their pollen-grain form; their visible characters are few and mostly of a negative nature. They show their distinction from those of group A in their lack of the broad rounded flecked furrows of that group, but they show their relationship to them, i.e., their position in the Nassauvinae, in the great length and generally more or less rounded ends and the sharp definition of their furrows.

The grains of *Pamphalea* and *Cleanthes* are of interest because, although unlike those of group A, their furrows taper conspicuously, they bear unmistakable flecks on their surface—small and somewhat indistinct, it is true, but none the less homologous with those of group A. This flecked character of their furrows clearly distinguishes them from those of the other members of group B, and suggests for them an intermediate position between the two groups.

The genus *Cleanthes* D. Don is not recognized by Bentham and Hooker, its species being included with *Trixis*. The pollen grains of the three species of *Cleanthes* which have been examined are all alike, and, except for their slightly flecked furrows, conform to our group B, and are quite distinct from those of *Trixis*. They differ from them in their sharply tapering fur-

rows, the much weaker development of the flecks, their spheroidal shape, and absence of polar elevations. Though there is nothing in the characters of the different species of *Cleanthes* to show that the genus is closely related to those of our section B, I believe that the absence from their grains of some of the most prominent characters of the five species of *Trixis*, is sufficient warrant for maintaining the genus *Cleanthes* separate from *Trixis*.

The grains of *Polyachyrus* (fig. 5), *Leuceria*, and *Moscharia* are essentially alike; they are small and spheroidal, with the exine perfectly smooth, and the furrows without flecks and tapering conspicuously towards their ends, which are, nevertheless, always more or less rounded.

From a consideration of the various characters of the pollen grains of the Nassauvinae and comparison with those of the other groups of the Compositae, certain lines of development are suggested. The fact that their grains are entirely without spines might be taken to indicate primitiveness, because the primitive form of a spore is smooth. Nevertheless the basic form of the pollen grain of the Compositae is unquestionably echinate. Thus the indication from this source is that the Nassauvinae may be either primitive or advanced, in fact at either one end of the development of the Compositae or at the other. The great achievement of the Composite pollen grain was the development of spines, which are quite the most conspicuous character of the grains of the majority of the species in all the tribes except the Mutisieae. Nevertheless the spines are found to be very minute or entirely absent in several widely separated groups. The cause of this smallness or absence of spines we do not always know, but certainly in some cases it is a suppression in response to the mode of pollination. For example in the Ambrosinae which are wind pollinated, I have shown (1928a) that a complete series of forms is found, ranging from that of the fully echinate grain of *Oxytenia*—a monotypic genus—which is undoubtedly primitive for the Ambrosinae, to that of the much more advanced Euxanthium with grains possessing only the slightest vestiges of spines. Likewise among the Anthemideae (Wodehouse, 1926), the Artemisias and their allies, all of which are wind pollinated, are nearly or quite without spines, so that in these cases there is little doubt that

the smallness or absence of spines is a suppression in response to the anemophilous habit. On the other hand, the pollen grains of some groups of the Compositae which are not wind pollinated show a strong tendency towards a suppression of spines for no apparent reason. Among the Cynareae, the tribe which is probably most closely related to the Mutisieae, many species have grains with spines greatly reduced and even occasionally entirely absent, and in the Mutisieae all of the species which have been examined, except one, have the spines greatly reduced; nevertheless, vestiges of them can nearly always be found. In the Nassauvinae, however, no trace of them has been seen in any species. Thus it appears that the developmental tendency of the spines in the Cynareae and Mutisieae is that of suppression or reduction, culminating in their entire absence in the Nassauvinae. The only alternative possible is that the Nassauvinae represent the primitive group of the Compositae from which the others took their origin, but the ease with which the spines appear to be lost in the phylogeny of the Compositae makes it seem more likely that the pollen grains of the Nassauvinae are advanced rather than primitive.

The furrow exists in all possible forms in the different tribes of the Compositae. I have shown (1928) that in the Ambrosinae the developmental tendency is a shortening of the furrow, starting with the long pointed form of the grain of *Oxytenia*, and ending with the short rounded form of *Ambrosia* and *Xanthium*. In the genera and species of the Cynareae, both the length and definition of the furrows are various and haphazard in distribution. In the grains of *Cousinia*, for example, the furrow is long, but shallow and imperfectly defined, with the surface of the intine shading gradually into that of the furrow; in *Carduus divaricatus* the furrow is medium in length, but clearly and sharply defined; in the grains of *Centrophyllum* it is so short that it practically coincides with the germinal pore; and in the genus *Centaurea* all lengths, and variation in definition may be found. Thus in the Cynareae no definite tendency is seen; the furrows are phylogenetically unstable.

In the Mutisieae, on the other hand, there is a definite tendency towards the lengthening of the furrow; in nearly all it is long, and in the subtribe Nassauvinae the lengthening is carried to its greatest extent, for in the grains of all species of

this group we have seen that the furrows almost meet at the poles, and in those of *Trixis* they are carried even beyond into the polar elevations. Furthermore in the grains of all the Nassauvinae the furrows are sharply defined; the transition in tissue from that of the general surface to that of the furrow is abrupt and the furrow is sunken so that there is no gradual change in texture in passing from one to the other, as is frequently encountered in the grains of the neighboring subtribes. The relation of the sides of the furrow to its surface in the grains of the Nassauvinae calls to mind the lids covering the ball of the mammalian eye. This reaches its best development in the grains of *Jungia*, in which the margins of the furrow bear an undulating frill, just as the lids of the eye bear lashes. A shortcoming of the analogy is that in opening, the margins of the furrows stretch the delicate membrane crossing the surface, instead of sliding over it as the lids slide over the ball of the eye.

Summarizing, it appears that the Nassauvinae may represent the culmination of three more or less distinct developmental tendencies, viz., the reduction of spines observed all through the Cynareae and Mutisieae, culminating in the entire absence of spines throughout this group; the lengthening of the furrows seen in various stages of development in the other tribes of the Mutisieae, culminating in the grains of *Trixis*; and the definition of the furrows strongly felt in the Nassauvinae, culminating in the marginate grains of *Jungia*. On the basis of the morphology of their pollen grains, the different genera of the Nassauvinae appear to be closely related and represent the end of a phylogenetic line of the Mutisieae.

YONKERS, NEW YORK

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Explanation of plate 3

All figures were drawn free-hand from studies made with a Zeiss apochromatic objective, 2 mm., Na. 1.3 and a 10× compensating ocular, resultant magnification 900. No constant magnification is employed in reproduction. Instead a size is adopted sufficient to show the important characters. The dimensions given are the average transverse measurements; in elongate or flattened grains, the average transverse and average axial measurements.

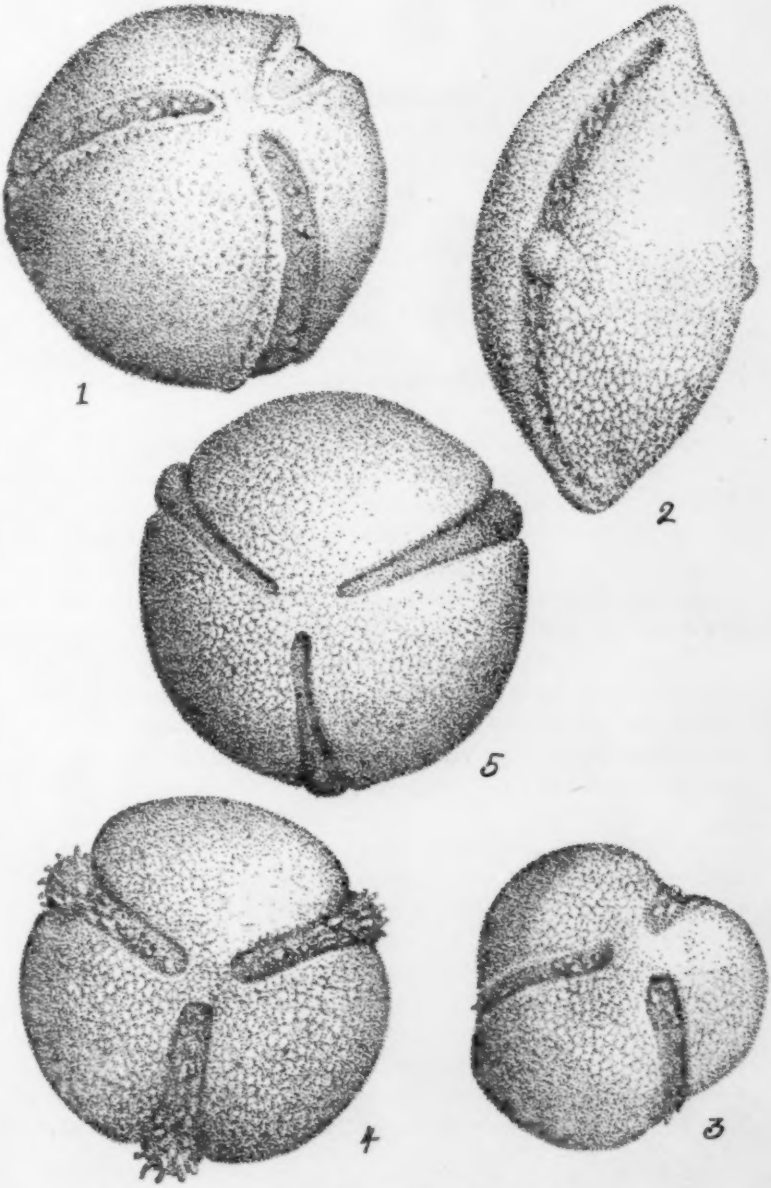
Fig. 1. Pollen grain of *Jungia floribunda* Less. 25.8μ diam. Viewed slightly to one side of the pole, showing the long rounded flecked furrows with projecting margins.

Fig. 2. Pollen grain of *Trixis corymbosa* D. Don. 30.0μ×43.3μ. Side view showing the long rounded and flecked furrows, extending into the polar elevations.

Fig. 3. Pollen grain of *Trixis corymbosa* viewed slightly to one side of the pole, showing the closely approaching ends of the long furrows.

Fig. 4. Pollen grain of *Triptilion euphrasioides* DC. 18.5μ diam. Polar view, showing the rounded ends of the long flecked furrows almost meeting at the pole.

Fig. 5. Pollen grain of *Polyachyrus sphaerocephalus* D. Don. 27.5μ diam. Polar view, showing the long tapering furrows with rounded tips, but without flecks.



POLLEN GRAINS OF NASSAUVINAE

UNIV. OF MICH.

A double-walled pot for the auto-irrigation of plants[1]

J. Dean Wilson

(with three text figures)

In growing plants in pots for experimental or commercial purposes, it is frequently desirable to control or maintain the percentage of moisture in the soil more closely than can be done by the usual method of watering at one or two-day intervals. This can now be done very satisfactorily by the use of porous porcelain auto-irrigators (Livingston, 6, 8). By using these instruments in a number of pots with the same kind of soil, the irrigators being connected in series so that all draw water from the same reservoir and against the same resistance, it is possible to maintain the moisture content of all the pots at very nearly the same value. This may be done for long periods of time with a minimum of labor, after the necessary arrangements have been made at the start (Deatrick, 2; Dustman, 3; Livingston and Hawkins, 9; Livingston, Hemmi, and Wilson, 10). If several pots be filled with the same type of soil, each may be maintained at a different moisture content by using a mercury barostat of different height in each water system (Livingston, Hemmi, and Wilson, 10). Also, pots filled with soils of different physical characteristics and different water-holding capacities may be held at approximately the same water contents (on the basis of dry weight or dry volume) by allowing them to come into equilibrium with barostats of properly selected heights (Holmes, 5; Livingston, Hemmi, and Wilson, 10).

The auto-irrigator, as first used (Hawkins, 4; Livingston, 6; Livingston and Hawkins, 9) consisted of a cylindrical porous-porcelain cup, which was usually placed in an upright position in the mass of soil to be watered. This type was subject to difficulties, however, since the soil mass in which the irrigator was 'planted' sometimes lost its capillary contact with parts of the outer surface of the porous-porcelain wall, and successful operation requires that the porcelain-soil inter-face must be maintained, in order that the hydrostatic pressures existent in the water films of the soil mass may be quickly transferred

[1] Published with the approval of the Director of the Ohio Agricultural Experiment Station.

to those in the porous wall. A distinct improvement was introduced when the porous-porcelain cylinder was replaced by a cone of like material. When cones are used, capillary contact with the soil is maintained by gravity action, for the soil mass tends always to settle against the conical surface, and the contact between porcelain and soil should improve as time goes on.

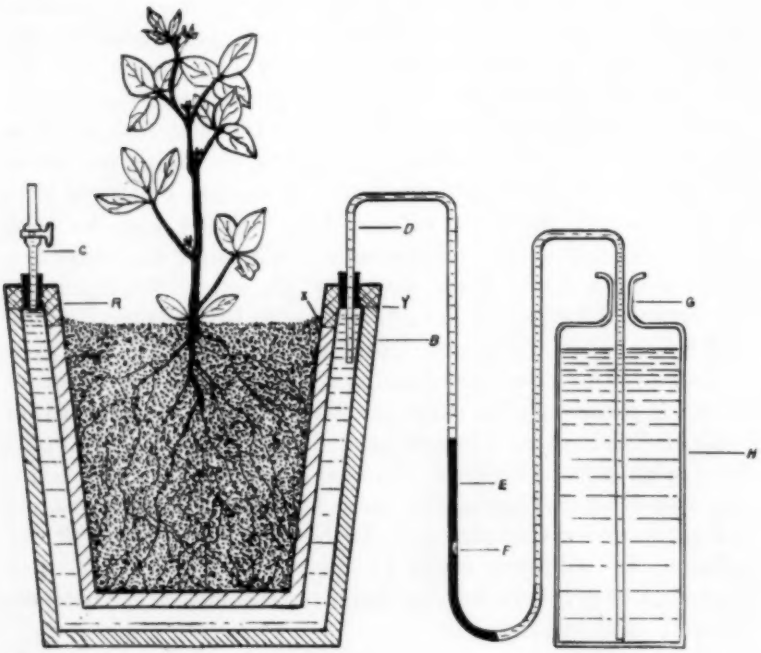


Fig. 1. Sketch showing details of a double-walled pot for the auto-irrigation of plants. This arrangement provides for the accurate determination of increments of water loss and the use of mercury barostats of widely varying heights.

Auto-irrigator cones operate best when placed centrally in the pot of soil, thus occupying the position in which it is usually desirable to place the plant. Both cone and plant cannot occupy a central position in the soil mass, but when two or more plants are placed in the same container they may be arranged around the centrally placed cone. The cone itself

occupies a considerable volume and the container consequently holds less soil when a cone is used. For these reasons it would be desirable to arrange an auto-irrigator so that the entire volume of the container would be available for soil. This has been accomplished by constructing a double-walled pot, consisting of two separate pots fastened together, either before or after firing, in such a manner that the seal is air tight. The inner pot resembles those ordinarily used for plants except that it is freely porous to water but not to air. The outer pot, which is somewhat larger than the inner one to provide for a water space between the two, is porous to neither air nor water. Arranging the pots in this way amounts simply to turning the cone type of irrigator inside out, as it were, placing the soil on the inside and the water on the outside. The result is shown, diagrammatically, in figure 1.

The inner wall, against which the soil rests and from which it draws water, consists of a porous pottery material much like that of an ordinary flower pot. The outer wall is also of pottery but it is waterproofed, the waterproofing extending over the rim and down on the inner wall to a line (*X*), the level to which the pot is to be filled with soil. This double-walled pot is made in two parts, the inner pot (*A*) having a rim or flange by which it is attached to the outer pot (*B*) at (*Y*). The two parts may be fastened together before firing or they may be kept separate in the kiln and subsequently cemented together if preferred, the process of manufacture being thus simplified. The double hatched part of the diagram represents the waterproofed portion of the inner pot.

In operation, the space between the two walls is filled with water and the inner wall is thus kept saturated. The soil rests against the slightly conical surface of the inner wall and good capillary connection is accordingly maintained by gravity. The whole cavity of this type of irrigator is available for soil and the roots of plants, and a single plant may be placed centrally in the pot. The water-supplying surface is much larger than when an irrigator cone is employed; for a 6-inch pot the porous inner wall has a surface of about 625 sq. cm., while the porous area of an irrigator cone (usually used singly in 6-inch pots of the common type or in a sheet-metal cylinder of about the same size) is only about 170 sq. cm. This larger

water-supplying surface of the new irrigator is a distinct advantage. Also, the new type may be employed in smaller sizes than could be used with the 3-inch cone irrigators. It has been tested in the 5-inch and 6-inch sizes and the pots might probably be even larger than the latter size without danger that the moisture condition of the interior of the soil mass might not be satisfactorily maintained.

The principles of operation are the same as when an irrigator cone is employed. There are two vertical, cylindrical perforations (about 18 mm. in diameter) through the rim where the inner and outer walls of the double-walled pot join, these being on opposite sides of the pot. Rubber stoppers, each bearing a tube, are inserted in these perforations. One of these tubes (*C*) is provided with a stopcock and is used for the removal of air by suction when the pot is filled with water through (*D*) at the time the irrigator is started. The tube (*D*) connects with the water reservoir (*H*). These two tubes correspond to the two tubes ordinarily attached to the cone types of irrigator by a 2-hole stopper. When the apparatus is installed suction is applied at tube (*C*), with the cock open, until air ceases to emerge. Then, the cock is closed. The hydrostatic pressure causing water movement from the reservoir to the space between the pot walls is regulated by the mercury barostat (*E*), inserted in the supply tube. As water is removed from the soil mass by evaporation from its surface or by plant absorption, it is replaced by capillary movement into the soil from the saturated porous wall of the inner part of the pot. The water content of this wall is maintained by a requisite movement of water from the reservoir. Water movement past the mercury column of the barostat is usually made evident by small bubbles, as (*F*), that rise from time to time. When movement is very slow the bubbles may not appear. A barostat of this general form has been used in earlier porous porcelain types of auto-irrigators (Livingston, 8). The height of the mercury column must be adjusted to the type of soil used; in ordinary practice it should be only 2 to 5 cm. for sandy soils, and 5 to 15 cm. for clay soils.

The increments of water loss from the outer reservoir are ascertained by refilling the bottle to a mark on its neck (*G*) from time to time, record being made of the volume of water

added in each instance, as is done in operating irrigator cones, atmometers, etc. If increments of water loss from the pot are required, the whole apparatus may be weighed at intervals, or the weighings may be made with the pot on a balance and the reservoir otherwise supported near it, the barostat tube being free to move in the neck of the bottle. Also, the barostat may be connected to a tube in the reservoir by a piece of

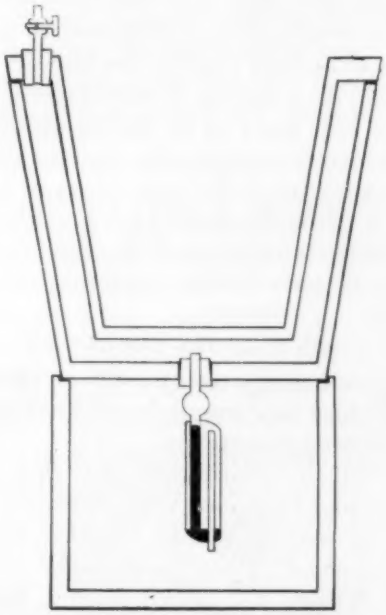


Fig. 2. A modified form of the pot shown in figure 1 in which a third pot supporting the others is used as a water reservoir. A special form of valve barostat is used here, the assembly being compact and easily movable.

flexible rubber tubing as was done in some of the experiments of Livingston and Hawkins (9). When it is desirable, the soil surface may be sealed to prevent evaporation.

The design of the irrigator shown in figure 1 was modified slightly for use in those cases where it is neither necessary to measure the amount of water used at definite intervals nor to use mercury barostats of extreme heights. This modified form is shown in figure 2.

It will be noticed that one of the holes formerly placed in the upper flange is now located in the base of the outer pot. A third pot of non-porous material serves as the outer water reservoir and also as a support for the double-walled irrigator pot. The inner reservoir is connected to the water-holding space of the lower pot by means of a specially designed barostat, as shown in the illustration. The height of the mercury column which may be used in this case is limited by the depth of the supporting pot. The ones first designed allowed for a barostat 8 cm. in height. This is sufficient to maintain all but the heavier soils at a water content low enough to be optimum for plant growth. An irrigator of this design is more compact and, in case the pots have to be moved about frequently, it eliminates the objection due to the semi-detached and somewhat unwieldy character of the outer reservoir used in the type shown in figure 1. However, it does not provide for an accurate means of measuring water losses at short intervals or for maintaining a series of pots having barostats of widely varying heights.

TESTS WITH THE IRRIGATORS

A variety of preliminary tests have been made to study the practicability of these new irrigators, and the results are given briefly in the following paragraphs.

Test 1. Two 6-inch auto-irrigator pots equipped with 5-cm. mercury columns and filled, one with muck and one with loam soil, unsealed and without plants, together with a standard, 5-cm. collodion-coated black atmometer (Livingston, 7; Livingston and Wilson, 11) placed nearby, were operated in a greenhouse for a number of weeks. Increments of water loss from each of the three reservoirs were determined at 5-day intervals and later reduced to losses in milligrams of water per square centimeter of surface area for each of the soils and the atmometer. Of course, it is understood that the spherical bulb of the atmometer and the circular, plane soil surface, the latter depressed slightly below the pot rim, were not affected alike by the environmental conditions influencing evaporation rates. The atmometer was used only to make a summation of the effect of the environmental influences affecting the evaporation rate, the results being useful in evaluating the varying losses from the two soils. The muck soil in this test consistently lost

more water per unit of surface than did the clay. Its black color gave it a greater absorptive capacity for heat than the clay possessed and its water content was somewhat higher than that of the latter, since both obtained their water past mercury columns 5-cm. in height. Each of these differences would favor a greater water loss from the muck. The atmometer lost water faster per unit of area than either of the soils. This was probably due, in part, to its very black color and thus high heat absorption, and, in part, to its more perfect exposure to conditions influencing the evaporation rate. The average for the four highest and also for the four lowest losses for 5-day intervals from each instrument are given in table 1.

TABLE 1

Losses in milligrams of water per square centimeter of exposed surface for 5-day intervals from a blackened atmometer, a muck, and a loam soil

	ATMOMETER	MUCK	LOAM
	mg.	mg.	mg.
Average of four highest values	375	312	276
Average of four lowest values	302	264	239

The losses from the three instruments for consecutive 5-day intervals paralleled each other very closely and maxima and minima occurred for the same intervals in each case. This indicates that the irrigators were able to maintain nearly constant soil moisture contents throughout the period of the test. If they have the ability to do this they should prove to be useful instruments for studying the relative rates of water loss by evaporation from the surfaces of different types of soil and through different surface mulches.

Test 2. In a comparison between irrigator losses and evaporation, measured by refilling the reservoirs to a mark on the neck each day, as was done in the preceding paragraphs, it is usually necessary to consider the lag that occurs between the time water is lost from the pot and the time it is taken up from the reservoir. To do this the pot and plant were mounted on a balance and the reservoir placed on the table beside it. A glass tube connected the pot with the water in the reservoir bottle, the tube being free to move in the neck of the bottle

without friction against the sides as the balance moved up and down. A blackened, spherical atmometer was placed on the same table near the balance. The pot was weighed and the reservoirs of the irrigator and atmometer were filled twice each day, at eight in the morning and four in the afternoon, for ten successive days. The results are shown in table 2.

TABLE 2

Mean daily water losses from irrigator pot, irrigator reservoir, and atmometer reservoir, determined at 8 a.m. and 4 p.m. each day for 10 days

	MEAN DAILY WATER LOSSES	
PART OF APPARATUS	4 P.M. TO 8 A.M	8 A.M. TO 4 P.M.
	cc.	*cc.*
Reservoir	38.3	18.5
Pot	19.4	40.0
Atmometer	12.6	26.5

The lag operated in this experiment in such a way as to make the rate of water loss from the pot two to three times as great as the loss from the reservoir for a few hours in the morning (when the evaporating power of the air was increasing), while in late afternoon and night the reservoir lost water most rapidly. The pot lost water about four times as rapidly during the day period used as during the night period, while the rate of loss from the reservoir continued at a rather constant rate throughout the 24-hour period, being but little different for the day and night periods when hourly averages are computed. This would indicate a rather constant hydrostatic pressure at the pot wall at all times, regardless of the rate of loss from the soil. The pot lost water at a rate that varied in a way corresponding to the losses from the blackened atmometer as would be expected.

In this experiment, if the variation in soil moisture content were calculated on the basis of dry soil weight, the variation in the water content of the auto-irrigated soil would be about 1.2 to 2 per cent, while, if the pot were watered once each day, the variation would be 5 to 7 per cent. These variations would be greater for large plants than small ones by either method. Whether the water losses are determined by weighing or re-

filling the reservoir, they should be made at the same time each day to get comparable results. This test serves to emphasize the fact that only the mean water contents of an auto-irrigated soil are maintained and not the absolute content. It also indicates, however, that watering by this method results in a much narrower range of variation than the method of bringing the pot weight back to the same value each day. Thus, when water losses are determined by reservoir readings for 5-day intervals, as was done in some of the tests reported in this paper, the daily rates are very little modified by possible errors due to the lag between pot and reservoir. In the case of the atmometer there is no appreciable lag (it occupies, at most, but a very few minutes even under the most rapid alterations of the evaporating power of the air) and it is quite safe always to consider reservoir loss as equal, increment by increment, to the corresponding loss from the atmometer sphere itself.

Test 3. Muck soil inoculated with the organism causing club-root of cabbage (*Plasmodiophora Brassicae* Wor.) was placed in four pairs of irrigator pots, each pair with a different barostat resistance, but the two pots of each pair alike; and cabbage plants were grown in the pots from February 6 to April 24, in the greenhouse. The four barostat resistances were 2 cm., 10 cm., 20 cm., and 30 cm. of mercury. The atmometer loss was nearly uniform throughout the period of this test, being about 100 cc. for each 6-day interval.

The plants with 10-cm., 20-cm., and 30-cm. columns all grew about alike and appeared healthy throughout the period. Those drawing their water against a barostat resistance of only 2 cm. of mercury grew more rapidly at first and possessed a healthy, vigorous appearance, being of a darker blue-green color than their companion plants, whose leaves were of a more yellowish green. After about two months these most freely watered plants began to show wilting on dry days and their irrigator losses became less than before. At the end of the experiment they were found to be infected with club-root, while there was no evidence of infection in the plants grown in drier soils. The wettest soils (with mercury columns only 2 cm. high, in which infection occurred) had a water content of about 50 per cent, on the basis of dry weight, and those

with the 10 cm. columns (in which no infection appeared) had a corresponding water content of only 18 per cent. It, consequently, appears that under the conditions of this experiment the critical moisture-content limit for infection, for the muck soil used, must have been between these two water-content values. With other lengths of barostat columns, between 2 cm. and 10 cm., the limits might have been defined more precisely.

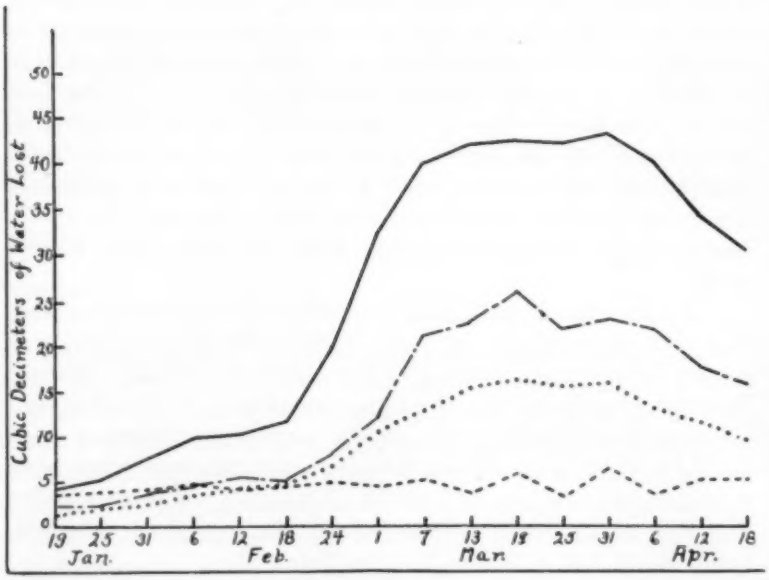


Fig. 3. Graphs showing the water losses for successive 6-day intervals from tomato plants in irrigator pots equipped with three different barostat heights and from a black, spherical atmometer. The losses corresponding to barostat heights of 5, 15 and 25 cm. are represented by the full, dot-dash, and dotted lines respectively. The atmometer losses are represented by the dash line.

This observation that cabbage is more susceptible to infection by the club-root fungus when the soil is wetter than when it is dryer than optimum, has been recorded in the literature several times (as by Chupp (1) and by Monteith (12) and others), and the result of the test here briefly described suggests that the auto-irrigator pot may be a valuable device for the study of such ecological relations.

Test 4. Three sets of 6-inch auto-irrigator pots, two in each set, all with the same loam soil, unsealed, and each with a tomato plant, but the sets with different mercury barostats, were operated in a greenhouse, together with a standard 5-cm. collodion-blackened, spherical atmometer. For one pair of pots the barostat columns were each 5 cm. high, for a second pair their height was 15 cm. and the third pair drew their water past columns of 24 cm. The increments of water loss were ascertained for 6-day intervals and each pair of corresponding values were averaged to give a single value for each interval for each pair of pots. The three resulting series of values for the pots and the single series for the blackened atmometer sphere were plotted and the four graphs thus obtained are shown in figure 3, each value being expressed in cubic decimeters.

Fluctuations in the rates of water loss, such as follow weather changes, are rather thoroughly smoothed out and obliterated by the use of the 6-day interval, and there is thus little correlation between the atmometer graph and those representing the irrigator losses. The latter all show an ascent to a maximum value and then a gradual descent. These changes were clearly not related to changes in the evaporation conditions of the greenhouse, as indicated by the atmometer graph. The steady increase in the size of the young plants and the corresponding additions to the areas of their leaf surfaces account for the ascending portions of the irrigator graphs. The exact causes for the decreasing values are less evident, but began about the time the plants flowered. Some of the lower leaves began to yellow at this time also, and the plants showed a slight drooping of the leaves on days of high evaporation. The latter fact would indicate that the pots were not supplying water at a rate equivalent to the demand set up by the large, succulent plants. It should be emphasized at this point that an irrigator of any size or type can deliver water only at a definite maximum rate corresponding mainly to the area of its porous surface and the conditions under which it is operated, such as height of mercury barostat, etc., and when a plant depending on the irrigator for its water has reached such a size that its needs are in excess of this delivery maximum, the plant will suffer from drought. Also the small mass of soil was possibly

not sufficient to supply nutrients at the necessary rate and this resulted in physiological changes within the plant which caused its water use to fall off.

The values for the 6-day increments showed pronounced and consistent differences according to the heights of the mercury column in the irrigator barostat. The ordinates of these three irrigator graphs doubtless represent approximately the transpiration rates of the corresponding plants, and also their vigor. The soil supplied with water against the lowest barostat pressure was clearly the wettest, and the plants in soils with that pressure (5 cm. of mercury) were the most vigorous and thrifty, indicating that the soil moisture content here was more nearly optimum than in those pots equipped with 15 cm. columns. The driest soil and the least vigorous plants correspond to the highest barostat pressure (25 cm. of mercury).

Test 5. A series of seven irrigator pots, filled with silt loam, were equipped with mercury barostats varying in height by 4-cm. intervals from 4 to 24 cm. The seventh pot in the series was watered with no resistance between the outer and inner reservoirs. This was done by arranging the outer reservoir so that its upper water level just corresponded with that of the bottom of the soil mass in the inner pot. Soy beans were planted in the pots and after the seedlings were well above the soil surface one good one was allowed to remain in each pot. The late fall and early winter season during which these plants were grown was found to be unfavorable to them and, consequently, the results were not all that was hoped for. However, there was a marked decrease in the rate of water use (loss from outer water reservoirs) from the wet to the dry end of the series, from 0 to 24 cm. of mercury column. A complete set of the data obtained is not given here, but in table 3 there are presented only the average daily losses for two 30-day periods (including losses from soil surface and plant leaves) for the pots equipped with barostat heights of 0, 12, and 24 cm.

The plants in the wet end of the series grew best, the one obtaining water against no mercury resistance being the largest in this test. Only one plant intermediate in the series was smaller than the one in the pot with the 24-cm. column. The reason for this break in the series was not determined. The

general appearance of the plants was also somewhat different in the wet and dry soils. The former were taller, had longer stem internodes and leaf petioles, and fewer axillary branches than the latter. The leaf number and size was much the same throughout the series, but the plants on the dry end blossomed and bore fruit more profusely than those with more available soil moisture. Some of the influences of different, maintained soil moisture contents on plant growth are shown in this test, and the irrigator pot appears to be an efficient instrument for providing such controlled moisture conditions.

Test 6. To compare the efficiency of the cone and pot types of irrigators, tomato plants were grown in soil watered by each

TABLE 3

Average daily water losses during two 30-day intervals from plants and soil in irrigator pots equipped with barostats of 0, 12 and 24 cm. in height

INTERVAL	BAROSTAT HEIGHT IN CENTIMETERS		
	0	12	24
	cc.	*cc.*	*cc.*
First	68	43	32
Second	95	67	49

instrument. Loam soil was placed in 6-inch irrigator pots and in 1-gallon tinned-metal cylinders, irrigator cones being 'planted' in the center of each of the latter. Mercury barostats 25 cm. in height were used in each arrangement. The water losses from soil and plant combined were determined at 3-day intervals over a period of two months for each type of irrigator. The results are not shown in detail, but when the average daily losses for three periods of 21 days each, covering most of the growth period of the tomato plants, were compared for each type of instrument, it was found that the losses from the pot type of irrigator were greater in every instance, but the plants watered by the cone nearly equaled the others in growth. The irrigator-pot was found to be somewhat easier to set up and operate than the cone, and may be considered an equal if not superior instrument tc the latter for irrigating plants over long

periods, because of the greater area of porous surface it provides for a given soil volume.

The experiments reported in the preceding paragraphs seem to indicate clearly that this new auto-irrigator pot has promise as a research tool in physiological, ecological, agricultural, and even pathological experimentation with plants where the maintenance of a fairly constant water-supplying power of the soil is desired.

The author wishes to acknowledge his indebtedness to Professor Arthur S. Watts, of the Ceramics Department of the Ohio State University, through whose courtesy these new pots were manufactured, and to Professor B. E. Livingston, of the Johns Hopkins University, for his criticisms of the manuscript.

SUMMARY

In growing plants for experimental purposes it is frequently desirable to regulate the soil moisture content more closely than can be done by the ordinary method of adding water at one- or two-day intervals. This has been done by the use of two pots, one placed inside the other and the two fastened together by means of a flanged rim on the inner one. The inner one is porous to water but not to air, and the outer one is porous to neither. The inner pot is enough smaller than the outer to provide for a water reservoir between the two.

This pot type of irrigator permits the placing of a plant in a central position in the soil mass in which it is to be grown, and provides a much larger area of porous wall in proportion to the volume of soil to be irrigated than is the case with the older types of auto-irrigators. Otherwise, the principles of operation are similar for the various types.

Several tests to determine the usefulness and practicability of this new type of irrigator have been made. These include the following studies: one on the comparative losses of water by evaporation from different soil types and a blackened atmometer; the time lag occurring between the loss of water from a pot and its absorption from the outside reservoir; another on the possibility of maintaining such soil-moisture contents that infection of cabbage by club-root will or will not occur; a third on the variations in the amount of water used when tomato plants obtain their water past mercury barostats

of different heights, and a similar experiment for soy beans, with notes on growth characteristics of the plants; and finally, a comparison between the pot and cone types of irrigators to determine their relative efficiency as irrigators.

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Development of the integument and germination of the seed of Eleusine indica

MARGARET P. CUMMINS

(WITH SEVEN TEXT FIGURES)

Eleusine indica Gaertner is one of the few grasses in which the integument develops as a hard seed coat while the pericarp remains as a thin, loose layer. Because of this, a detailed study of the development and fate of the integuments has been made. Since the seeds were found not to germinate under ordinary conditions, the effect of the seed coat on imbibition was also studied.

The nature and development of the integuments has been studied in *Poa pratensis* and *Poa compressa* by Miss Andersen (1), in *Holcus halepensis* by Harrington (8), in *Zea mays*, *Triticum vulgare*, and *Avena sativa* by True (13), in barley by Brenchley (2), in *Zea mays* by Weatherwax (15) and Guignard (7), in *Poa annua* by Golinski (6), and in *Triticum vulgare* by Jensen (10). In most of these the integuments disappear or are crushed beyond recognition before maturity of the seed; but in *Poa* (1) and *Holcus* (8) at least one of the integuments persists and forms an important part of the covering of the mature seed. The writer has found in the literature no reference to the development of the integument or to germination in *Eleusine*.

Material used in this study was collected at Bloomington, Indiana, in the summer and fall of 1927. This species is abundant in this locality in alleys, gardens, and waste ground.

The ovaries containing immature seeds were imbedded in paraffin and sectioned with the microtome. The mature seeds, which were too hard to be treated in this way, were attached to blocks of wood with glue and cut freehand under the binocular microscope.

The ovary of *Eleusine* is typical of the grasses. The wall is of irregular thickness, the thicker part being at the top. It consists of an outer epidermis and four or five rows of parenchyma cells (fig. 1). The ovule is attached to the side of the ovarian cavity with the micropyle turned toward the bottom.

Just before fertilization, when the embryo-sac is mature, both integuments surround the nucellus completely. Although in most grasses the edge of the outer integument is caught in the stylar canal (Weatherwax, 15, *fig. 2;* Golinski, 6, *pl. 2, fig. 18;* Guignard, 7, p. 43–44), in *Eleusine* it continues down almost as far as the inner integument and forms only a protuberance in the canal (fig. 2).

Each integument is composed of two layers of cells except near the micropyle, where there are sometimes three layers.

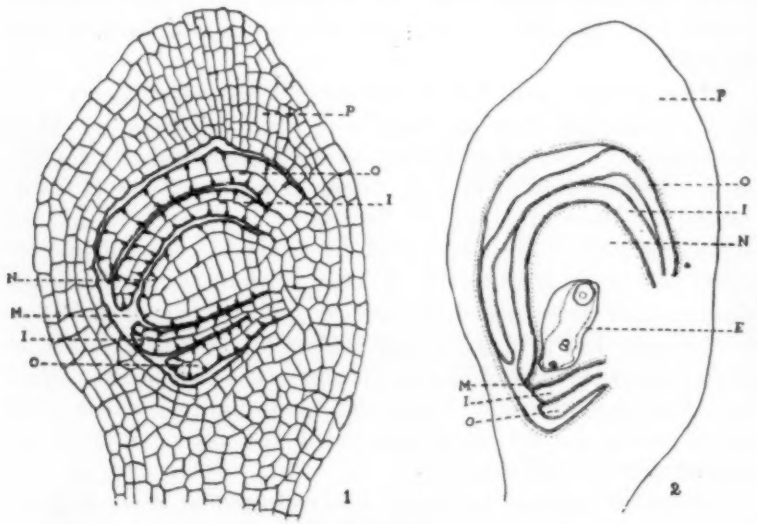

Fig. 1. Young ovary. Fig. 2. Ovary just before fertilization with both integuments surrounding the nucellus. *P*, pericarp; *O*, outer integument; *I*, inner integument; *N*, nucellar tissue; *M*, micropyle; *E*, embryo sac.

Long before fertilization the cells of the inner row of the inner integument are larger and stain more densely than the others (fig. 3). A radial lengthening of these cells is seen, especially at the chalazal end.

At the time of the four-nucleated stage of the germination of the megaspore the outer integument and pericarp are still present. Soon the outer integument begins to degenerate (fig. 4) and the pericarp shows signs of collapse. When the seed is nearly mature, the outer integument is gone, with the

pericarp persisting only as a thin layer, and the nucellus has been absorbed (fig. 5).

Mature seeds have a dark brown covering, two cells thick, formed from the inner integument. The pericarp is present only as a fibrous layer. The inner cells of the inner integument are rectangular in shape, with thick, hard walls. The outside cells have rounded walls, their outer walls being very much curved and thus forming the ridges seen on the seeds (fig. 6).

Seeds were gathered in October and kept in a warm, dry room in paper envelopes. An attempt to grow seedlings in the greenhouse in the winter was unsuccessful because the seeds

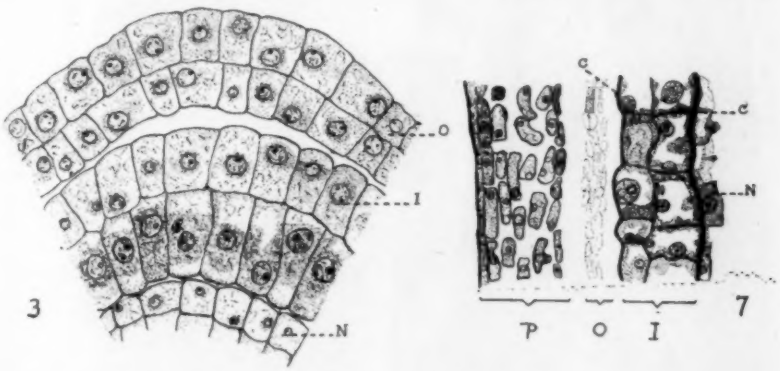

Fig. 3. Section of the outer and inner integuments, from an ovary of the same age as the one in fig. 2, showing the radial lengthening of the cells and darkening of the walls of the inner row of cells of the inner integument.

Fig. 7. Section through the seed coat with deposits of suberin or cutin shown by staining. *C*, cutin or suberin; symbols otherwise as in figs. 1, 2.

would not germinate. It was suspected that their failure to germinate was correlated with the character of the seed coat. Accordingly experiments on germination and microchemical tests of the seed coat were made.

In the experiments on germination certain methods and devices suggested by Crocker (3 & 4) were used. Dr. Eckerson's manual (5) and Tunmann's Microchemistry (14) were followed in making the chemical tests. Any tests depending upon color changes were difficult, because of the dark color of the seed coat, which resisted all attempts at bleaching.

In all the experiments on germination the seeds were placed on moist filter paper in crystallizing dishes. About thirty-five seeds were used in each lot treated, and the same number in a control in each case. The seeds used in the controls were gathered at the same time and kept as described before for the seeds used in the experiments, and therefore had not been affected by the forces of weathering. The experiments were

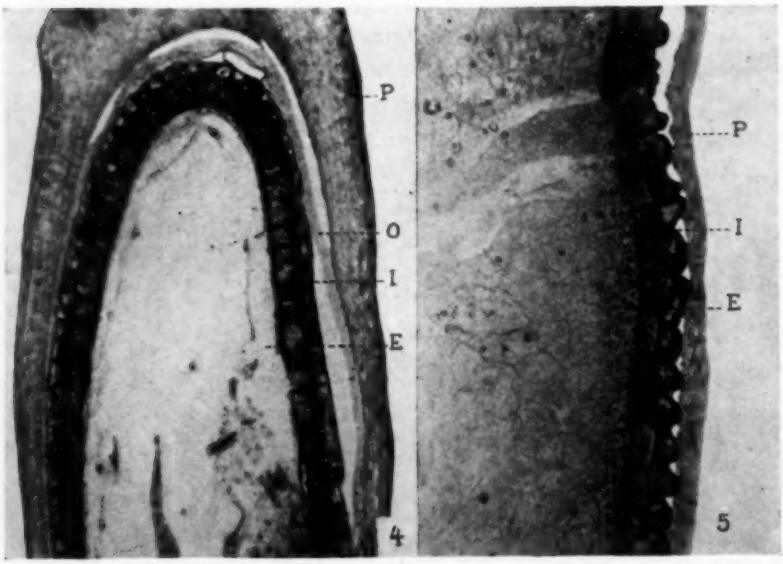

Fig. 4. Disintegrating outer integument. Fig. 5. Almost mature seeds showing the absence of the outer integument and the very thin pericarp. *P*, pericarp; *O*, outer integument; *I*, inner integument; *E*, endosperm.

started October 17 and the last one was performed January 21. Forcing agents suggested by Crocker (4) were used first.

Since some seeds will germinate after the seed coat has been scarified by some means, in the first experiment the seeds were rubbed between two pieces of fine sandpaper and placed in the germinating dish. In each of three lots so treated five or six seeds had germinated at the end of five days. One lot of seeds were mixed with sharp sand (about five hundred times as much sand as seeds), placed in a bottle, and shaken vigorously for

some time. Only one of these seeds germinated. Probably more would have germinated had the treatment been prolonged.

Since germination has been brought about thus far by physical changes, tests were made on the effects of freezing and thawing which seem to be of great significance in nature. Two different dishes were prepared. Each one was set outside on December 8. One was left outside a month. The other was brought inside three times during the month and placed near a radiator for two or three days. Thus it was subjected to great fluctuations in temperature,—from −22°C. to warm room temperature. The other seeds froze and thawed, but did not feel the great fluctuations in temperature. Both dishes were

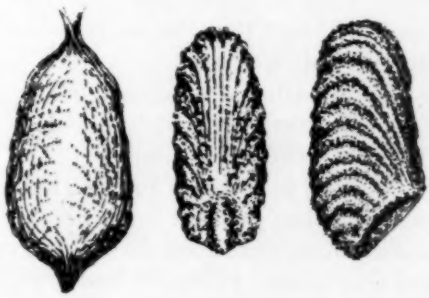

Fig. 6. Fruit and two views of the mature seed. Drawings made by Dr. Paul Weatherwax. ×25.

brought in and placed near the radiator at the end of the month. After four days six seeds had germinated in each dish.

From previous experiments it seemed probable that the mechanical resistance of the seed coat might be such that the pressure of the expanding embryo could not rupture it without aid. Hence to test the mechanical resistance and to modify the colloids of the seed coat, the seeds were immersed in boiling water for one minute and then put to germinate. No results were obtained, either because the seeds were not in the water long enough or the temperature of the water killed the embryos.

Soil as a substratum frequently forces the germination of dormant seeds. Soil may contain a number of reagents which play a part, each acting upon the seed coat or upon living structures. Accordingly some seeds were placed on soil. At the end of a week one seed had germinated.

Seeds were immersed in an oxidizing agent, commercial hydrogen peroxide, and left for one-half day before being put to germinate. Not one germinated. Some other seeds were immersed in alcohol and left one-half hour before being put to germinate. None of these germinated. One lot of seeds were immersed in ether for ten minutes and another lot for forty minutes. After twenty days two seeds from the latter lot had germinated.

Near the middle of January some soil was taken from the place where *Eleusine* had grown the year before, and was kept moist in the greenhouse. In a week many seedlings appeared.

Seeds used in the controls carried on with these experiments gave uniformly negative results except in one case, where a single seed germinated. The fact that the seeds germinated from the very first if scarified showed that time for after-ripening was not necessary. Germination was delayed because of the nature of the seed coat. The need seemed to be for certain physical conditions rather than chemical stimuli.

Since the seed coats were found to be so hard that germination was impossible unless the seed coats were modified in some way, microchemical tests were made on the seed coat. The main parts of the seed coat seemed to be cellulose and suberin or cutin. Both Sudan III and a Scarlet R showed cutin or suberin present on the inner and outer surfaces of the integument and epidermis of the pericarp. In using either of these stains a drop of the solution was placed on the slide and after twenty minutes washed with 50 per cent alcohol (Eckerson, 5). The sections were then observed in glycerine. In using these stains, both the inner and outer surfaces of the integument and the epidermis stained red. The band of red on the inner surface of the integument was much thicker than that of the outer (fig. 7). A little red appeared in the cross walls which gave the appearance of suberin or some fatty substance. A chlorophyll solution (Harrington, 9) showed a tinge of green on the outer walls of the cells of the seed coat. This test was not satisfactory because the depth of the green could not be determined on account of the dark color of the seeds, but it seemed to indicate the presence of cutin or suberin in the outer walls. A solution of iodine (Strasburger & Hillhouse, 12) gave a starch reaction in almost all the pericarp. The degenerating outer integument

turned reddish brown, indicating a partial hydrolysis of the original cellulose. When an *Eleusine* slide was treated with iodine, washed well with distilled water, and 75 per cent sulphuric acid was added, the radial walls of the integument, the placenta, and a small part of the pericarp gave a cellulose reaction, turning blue or partly dissolving (Eckerson, 5). Immersing the seeds in concentrated sulphuric acid for six days caused the seed coats to become soft and brittle. On account of the black color added to the original dark color by these reagents it was impossible to tell what parts of the seed coat had been dissolved.

SUMMARY

In *Eleusine* the edge of the outer integument is not caught in the stylar canal as it is in most grasses. The integument continues on down to the micropyle and forms only a protuberance in the canal.

At the time of the four-nucleated embryo-sac the outer integument shows signs of absorption, giving the dextrin reaction, and at maturity it has been absorbed.

The inner integument completely surrounds the nucellus when the embryo-sac is mature. It consists of two layers of cells. The inner and outer surfaces of the integument are cutinized or suberized. The inner of these layers is much thicker. The cross walls are mainly cellulose.

The inner integument develops into a hard, grooved seed coat with the pericarp persisting only as a broken layer.

Seeds of *Eleusine* will not germinate until after the seed coat has been modified in some way. Failure to germinate apparently is not due to immaturity of the embryo. Freezing and thawing are natural forcing agents. Repeated fluctuations in temperature are not necessary. Scarifying the seed coat by different means gives good results in germination.

I take opportunity here to express my obligations to Dr. Paul Weatherwax for the suggestion of this problem and for assistance and criticism in connection with this study.

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New plants from Nevada

PHILIP A. MUNZ

During the past four seasons Mr. Edmund C. Jaeger of the Junior College at Riverside, California has made profitable trips to the Charleston Mountains in extreme southern Nevada. Among the very interesting plants that he and others have recently obtained in this isolated mountain range, the following species have been carefully studied and found worthy of description.

In this connection I wish to acknowledge my indebtedness to Dr. Ivan M. Johnston of the Gray Herbarium for kindly comparing these plants with material there, and to Dr. E. B. Copeland of the University of California Herbarium for loan of a collection of *Epilobium nivium* Brandegee, namely one from St. Johns Peak, Lake Co., California, by *W. W. Mackie* in 1902, and for comparison of this loan with the type collection.

Lesquerella Hitchcockii Munz, n. sp. Perennial, silvery stellate throughout, stellae small with rays numerous and irregularly coherent; caudex much branched; stems ascending, 1–4 cm. long, unbranched; radical leaves varying from oblong or oblanceolate and with entire blades 5–8 mm. long, ca. 2 mm. wide, obtuse, and narrowed into slender petioles of same length, to broadly ovate or oblong, with blades 4–5 mm. long, 3–4 mm. wide, on somewhat shorter petioles; cauline leaves reduced, few, narrower; flowering stems 1–1.5 cm. long; subscapose, with terminal few-flowered corymbs; sepals 4–5 mm. long; petals pale yellow, linear-spatulate, 5–7 mm. long; filaments linear; fruiting stems 2–4 cm. long; fruits 3–8 in subcorymbose terminal cluster; pedicels stellate, ascending, not usually markedly sigmoid, 3.5–5. mm. long; capsules subglobose, not noticeably compressed, substipitate, reddish, glabrous, 3–4 mm. long, with entire septum; ovules 2–4 in each cell; styles filiform, reddish, 4.5–5 mm. long; seeds ca. 2 mm. long, brown, not winged.

Planta perennis, argenteo-stellata; foliis oblanceolatis aut ovato-oblongis, laminis 4–6 (8) mm. longis, 2–4 mm. latis; caulibus cum capsulis subscaposis, 2–4 cm. longis; floribus paucis, subluteis, corymbosis; capsulis subglobosis, glabris, subrubris, substipitatis, 3–4 mm. longis; stylis 4.5–5 mm. longis; seminibus non alatis, ca. 2 mm. longis.

Type, fruiting plants from high exposed ridges in the Charleston Mountains of Nevada, at 10,500 ft. alt., collected by *E. C. Jaeger* and *C. L. Hitchcock*, Sept. 1, 1927 (Pomona College Herbarium No. 45092). An earlier collection in flower, same region, *E. C. Jaeger*, June 26, 1926 (Pomona). In the herbarium at Pomona College are two sheets from southern Utah with the smooth reddish fruits of the proposed species. One from Marysvale, *M. E. Jones 5404*, has styles of same general length and rather narrower leaves. The second from Panguitch, *Jones* on July 18, 1920, has styles only 3 mm. or less long and narrow leaves. Both these plants are rather small and depauperate specimens, scarcely or not at all scapose, yet with the fruit of *L. Hitchcockii*. They differ from all other sheets I have seen from Utah, and indicate the need of more material from that region.

I take pleasure in naming this species for Mr. Charles Leo Hitchcock, one of my students, from whom more will be heard in Botany. The smooth fruits and low habit separate this species from others of the region.

Draba Jaegeri Munz & Johnston, n. sp. Caespitose perennial; caudex often much and loosely branched; leaves more or less tufted, narrowly obovate, acutish to obtuse, 4–6 mm. long, 3–4 mm. wide, thickened and with indistinct midvein, pubescence rather loosely stellate, marginal cilia evident, leaves grayish but not silvery; scapes slender, pubescent, 2–5 cm. long; flowers showy, in a dense corymbose raceme 1–1.5 cm. long; sepals pubescent, purplish, hyaline margined, 2.5 mm. long; petals white, 5–6 mm. long; fruiting inflorescence not elongated; pedicels 4–6 mm. long; capsules flattened, densely stellate-pubescent, 4–6 mm. long, 3–4 mm. broad; styles filiform, 3–4 mm. long, dark; seeds brown, 1 mm. long, not winged.

Planta perennis, caespitosa; foliis cristatis, anguste obovatis, stellato-pilosis, ciliosis, 4–6 mm. longis, 3–4 mm. latis; scapis tenuibus, pubescentibus, 2–5 cm. longis; floribus spectabilibus; sepalis subpurpureis, pubescentibus; petalis albis, 5–6 mm. longis; pedicellis 4–6 mm. longis; capsulis complanatis, stellato-pubescentibus, 3–4 mm. latis; stylis 3–4 mm. longis; seminibus non alatis, 1 mm. longis.

Type, from Charleston Mts., in rock crevices at 11,000 ft. alt., *E. C. Jaeger*, June 26, 1926 (Pomona College Herbarium No. 44,771). A second collection from 10,000 ft. alt. by *E. C. Jaeger* was taken the same day (Pomona).

In Payson's key to the perennial scapose Drabas of North America (Amer. Jour. Bot. **4**: 256. 1917) this species would be near to Payson's *vestita* (correct name, *D. Paysonii* Macbr.), but has leaves too wide. It might run also to his *D. Mulfordae*, from Idaho, but again the leaves are about twice as wide as in that species. The leaves and habit suggest *D. uncinalis* Rydberg, which is placed by Payson in the smooth-fruited species. He had not seen material for that species, but the co-type at Pomona College has ample pubescence on the fruits. The proposed species differs from *D. uncinalis* by its larger fruits and longer styles. In fact the very long styles set *D. Jaegeri* apart from all closely related species, exceeding even those of *D. pterosperma*, which differs by having winged seeds.

Ivesia Jaegeri Munz & Johnston, n. sp. Green, perennial, villous and minutely glandular throughout, but not viscid; caudex woody, 2–3 cm. long, 7–8 mm. thick, crowned with persistent leaves and stems of previous years; stems several, slender, simple below, sparsely and openly branched above, spreading, ascending at tips, 2–15 cm. long; stipules 6–8 mm. long, the free portion 2–3 mm. long, lance-linear, entire; leaves pinnate, mostly basal; lower leaves with blades 1–5 cm. long; petioles 0.5–4 cm. long; leaflets 3–7 pairs, but not usually opposite, not crowded, 3–7 mm. long, divided almost to base into 3 or 4 oblanceolate to narrowly obovate segments, not bristle tipped, but frequently with 2–3 longer hairs at tips; upper leaves reduced, with 1–5 entire or somewhat divided segments, subsessile; flowers in 2–5 flowered open cymes; pedicels filiform, 0.5–2 cm. long; hypanthium saucer-shaped, 3–4 mm. wide; bractlets lanceolate, 2 mm. long; sepals ovate, 3 mm. long; petals yellow, narrow, oblanceolate, 2 mm. long, scarcely clawed; stamens 20, filaments linear, ca. 2 mm. long, seated close to the styles; receptacle hairy; pistils ca. 9; styles filiform, almost apical, ca. 2 mm. long; achenes brown, glabrous, scarcely 1 mm. long.

Perennis, viridis, villosus, vix glandulosus; caulibus aliquibus, tenuibus, subdecumbentibus, 2–15 cm. longis, ex caudice ligneo; foliis pinnatis, 1–5 cm. longis, cum 3–7 paribus pinnarum; pinnis 3–7 mm. longis, partitis, oblanceolatis aut anguste obovatis; floribus 2–5, in cymis laxis; hypanthio breve crateriformi, 3–4 mm. lato; sepalis ovatis, 3 mm. longis; petalis luteis, angustis, oblanceolatis, 2 mm. longis; staminibus 20; pistillis ca. 9; stylis linearibus, subapicalibus, 2 mm. longis; acheniis glabris, 1 mm. longis.

Type, Charleston Resort, Charleston Mts., July 3, 1927, *Marcus E. Jones* (Pomona College Herbarium No. 44, 277; isotypes at University of California, Gray Herbarium, and New York Botanical Garden). Known also from the following collections: limestone rocks, Charleston Mts., *Jaeger*, Sept. 12, 1925 (Pomona); at 10,000 ft., *Jaeger*, June 20, 1927 (Pomona); and Little Falls near Griffith's Resort, Kyle Canyon, Charleston Mts., *Jaeger*, Sept. 1, 1927 (Pomona). The species first came to my attention through the 1925 collection by Mr. Jaeger, and it is a pleasure to name it in his honor.

It is rather an interesting species in combining characters of *Ivesia* and *Potentilla* proper. Its general aspect is that of *Ivesia Baileyi* with foliage and habit like that species, but the number of stamens (20 instead of 5), the more filiform filaments, the position of the stamens near the pistils instead of being separated by an open space, and the rather subapical insertion of the style are more like *Potentilla*. The new species is less viscid-glandular than *I. Baileyi* or *I. setosa*.

Epilobium nevadense Munz, n. sp. Low, suffruticose, caespitose, with freely branched woody caudex, these branches prostrate, dark brown, with freely exfoliating bark, and 2.5–3 mm. thick, giving rise to many slender, erect, pubescent, mostly simple stems, which are straw-colored, often purplish-tinged, 12–25 cm. high, leafy throughout; leaves glabrate, glaucescent, denticulate, green or purplish, on short pubescent petioles and tipped with inconspicuous stout rigid gland; lower leaf-blades oblong, obtuse, opposite, 8–15 mm. long, 2–3 mm. wide, on petioles 2–3 mm. long; main cauline leaves alternate, somewhat narrower and more acute, gradually reduced upward, with fascicles of bract-like leaves in axils; leaves of inflorescence reduced to linear bracts 2–5 mm. long; flowers several on each stem, in loose racemes, sessile or on short glandular pedicel-like stems, each with small bract near base of glandular ovary; calyx tube glandular without, glabrous within, 2–3 mm. long, tinged reddish, tubular, slightly enlarged above ovary; calyx-lobes lanceolate, glandular, 3–5 mm. long, reddish, deflexed in anthesis; petals violet-purple, obcordate, 6–7 mm. long; stamens with filaments not dilated, the longer ones ca. 3 mm. long, shorter ones ca. 1.5 mm. long; anthers apiculate, 0.5 mm. long; style glabrous, ca. 10 mm. long; stigmas ca. 1 mm. broad, squarish in outline, with 4 subtriangular reflexed lobes; capsules subfusiform, glandular-pubescent, 8–12 mm. long, 1.5–2 mm. thick; the few seeds develop-

ing near the center, seeds smooth, brown, ca. 1.5 mm. long; coma white, about 5 mm. long.

Humilis, suffruticosa, caespitosa; ramis caudicis prostratis; caulibus tenuibus, erectis, pubescentibus, foliosis, 12–25 cm. altis; foliis glabris, glaucescentibus, denticulatis, linearibus aut suboblongis, 8–15 mm. longis, 2–3 mm. latis; pedicellis glandulosis; floribus in racemis; hypanthio glanduloso, 2–3 mm. longo, subpurpureo; lobis calycis lanceolatis, glandulosis, 3–5 mm. longis; petalis purpureis, obcordatis, 6–7 mm. longis; staminibus 1.5 aut 3 mm. longis; stylis glabris, ca. 10 mm. longis, stigmatibus quadrilobatis; capsulis subfusiformibus, 8–12 mm. longis, 1.5–2 mm. crassis; seminibus paucis, fuscis, 1.5 mm. longis; coma alba.

Type, from Cathedral Rock, Charleston Mts., Nevada, at 9200 ft. alt., Sept. 4, 1927, *E. C. Jaeger* (Pomona College Herbarium No. 152,780; isotypes at University of California and Gray). An earlier collection at 8000 ft. was made Sept. 12, 1925, *Jaeger* (Pomona). This interesting species is very close to *E. nivium* Brandegee from Lake County, California. Both have the same general habit and stature; *E. nevadense*, however, has denticulate, glaucescent leaves rather than entire pubescent ones. The leaves are also narrower. *E. nevadense* has the flowers more glandular, and of different proportion, the calyx-tube being about half as long as in *E. nivium*, although the flowers are near the same general size. The coma is white instead of 'dingy'. The emphasis placed by Brandegee on the stout, rigid gland at the apex of the leaves seems rather unwarranted, since this same structure (at most rather inconspicuous) occurs also in *E. nevadense* and *E. paniculatum*, to which annual species both *E. nivium* and *E. nevadense* are undoubtedly related.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1926–1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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